CONFLICTING FLOWS THE DYNAMICS OF MYCELIAL TERRITORIALITY

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The Production Team

For many people, a fascination with fungi begins with their often colourful, curiously shaped fruit bodies, that bring forth images of food, fear and fantasy. Fruit bodies are, however, a bit like some film stars. Whilst attracting attention, their function is purely disseminative. They are the determinate and dependent offshoots from the less glamorous, behind the scenes production team, that does all the hard work needed to take in energy and convert it into a viable output.

With regard to fungi, there is perhaps a natural tendency to regard this production team, the mycelium, as a boring, uniformly absorbent mass of hyphal threads which, whilst important in energy capture, only really becomes interesting when parts of it aggregate and differentiate into a fruit body. I think that this view is mistaken, and, though not suggesting I am alone, I have increasingly come to regard the mycelium as a heterogeneous army of hyphal troops, variously equipped for different roles and in varying degrees of communication with one another. Without a commander, other than the dictates of their environmental circumstances, these troops organise themselves into a beautifully open-ended or indeterminate dynamic structure that can continually respond to changing demands. Recall that during its potentially indefinite life, a mycelial army may migrate between energy depots; absorb easily assimilable resources such as sugars; digest refractory resources such as lignocellulose; mate, compete and do battle with neighbours; adjust to changing microclimatic conditions; and reproduce.

Versatile Patterns

The versatility that enables a mycelium to undertake all these tasks, not necessarily in a fully predictable sequence, parallels that seen in some social collectives, such as those of army ants (Rayner and Franks, 1987). These systems might seem very different from one another in that in the mycelium it is the *development* of an individual *organism* rather than, as in army ants, the *behaviour* of a *grouping* of individuals that is versatile. However, logistically, this difference may simply be a function of where we as human beings draw the line between individuals and groups and, correspondingly, between determinate and indeterminate development. Both systems contain dynamically *interconnected*, partially autonomous entities, hyphae and ants, and both produce diverse organisational

patterns due to the complementary tendencies of these entities to associate and dissociate. These patterns can be extraordinarily similar, not only to one another but to many elsewhere in biology, and beyond. Such similarities suggest that the same "ground rules" or logistic procedures govern the association and dissociation of the partially autonomous entities comprising dynamic systems, regardless of the material nature of these entities. Moreover, by looking closely at the patterns, and identifying their recurrent features, it may be possible to gain insights into how these ground rules operate in practice. That is the exciting prospect that I think can be realized by carefully observing mycelial patterns.

Where can mycelial patterns best be observed? The standard answer might be in a Petri dish culture, but the homogeneous conditions encountered therein probably amount to a severe sensory deprivation for an organism thriving on environmental heterogeneity and uncertainty. For a full appreciation of versatility, it is therefore important, alongside pure culture studies, to observe mycelial patterns in natural settings, or, at least, under artificial or semi-natural conditions that simulate some aspect of environmental heterogeneity.

This is not as difficult as it might sound. Although the mycelial lives of fungi are often supposed to be conducted in secret, hidden within the opaque places where they find their food, many can be uncovered using little or no technology and just some knowledge of where and how to look. For example, wander into the forest, turn over a few logs, uproot some stumps and carefully peel away layers of leaf litter and a rich array of mycelial forms, the communicating pipelines of the ecosystem, comes into view. Many may contain hyphae aggregated into systems of cords or rhizomorphs (Figs. 1,2). Some of these can be traced out over distances of many meters, e.g., *Tricholomopsis platyphylla* and *Steccherinum fimbriatum* (Thompson & Rayner,1983). Others may form dense patches, e.g., *Marasmius wynnei* (Cooke & Rayner, 1984) or fairy rings with a polarized margin and degenerating trailing edge, e.g., *Clitocybe nebularis* (Dowson *et al.*, 1989; Figs. 3,4). Cut open some decaying wood: the decay and staining patterns revealed directly reflect the distribution of the mycelial armies they contain. Incubate the wood in a polythene bag for a few days and identifiable mycelia will often grow out directly over the surface (e.g., Rayner and Todd, 1979; Fig. 5). Take some soil home (or to the laboratory), put it in a transparent container and inoculate it with wood

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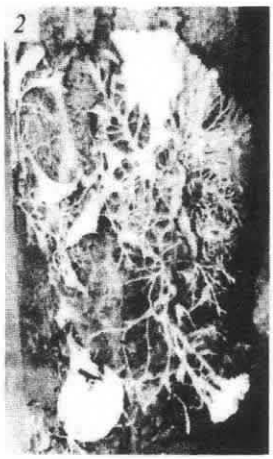
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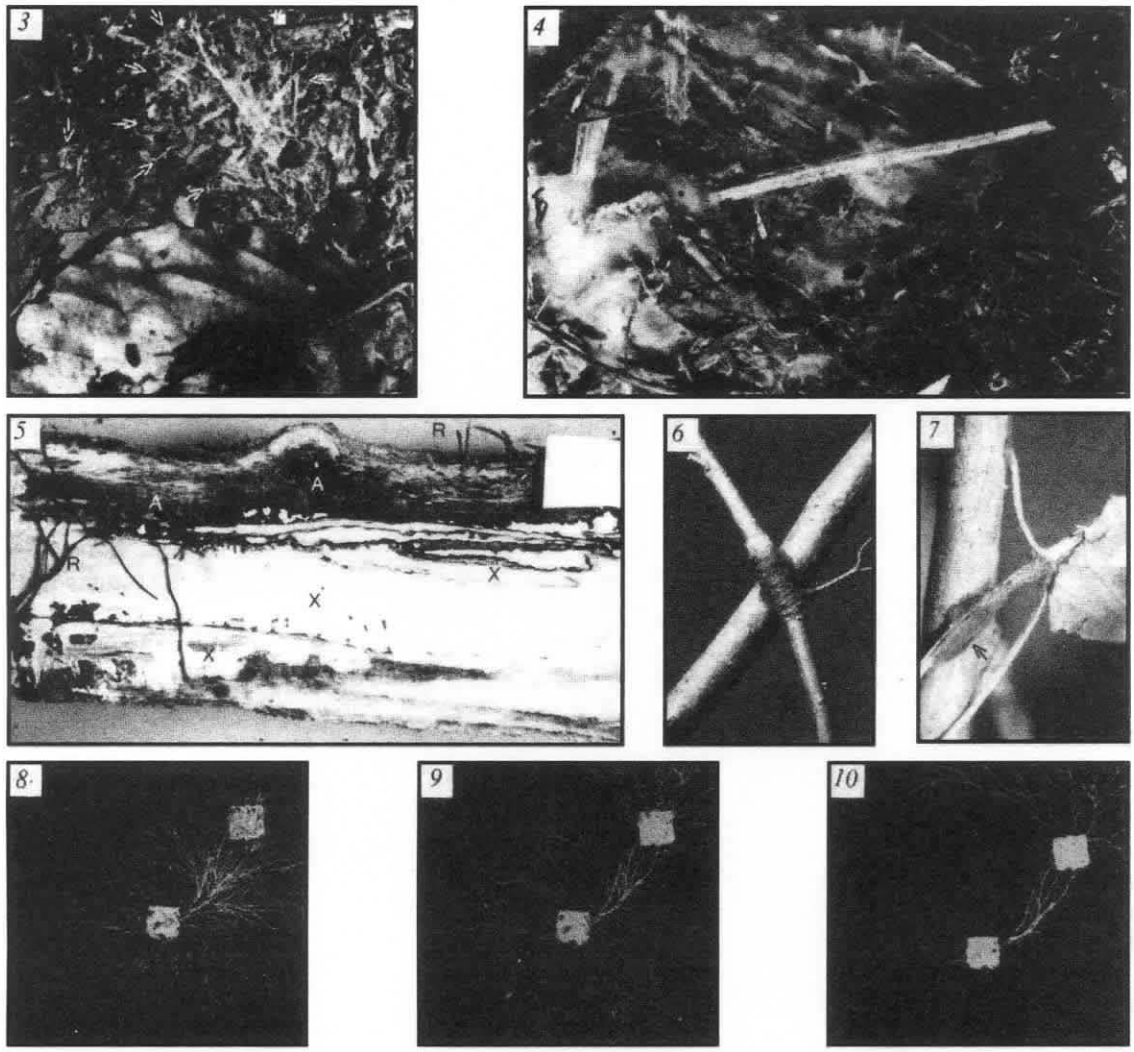


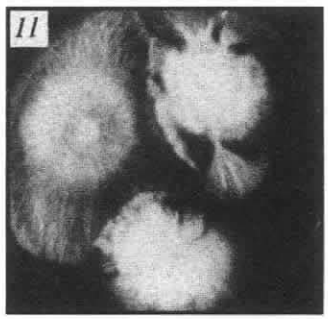
Figs. 1-10. Natural mycelial patterns. Fig. 1. Part of an excavated mycelial cord system of *Phanerochaete laevis* in beech (*Fagus sylvatica*) litter (from Thompson and Rayner, 1982) . Fig. 2 . Mycelial cords of *Phallus impudicus* on a beech log (from Coates and Rayner, 1985a). Fig. 3. Mycelial cords (arrowed) at the advancing front of a fairy ring of *Clitocybe nebularis* in beech litter (from Dowson *et al.*, 1989). Fig. 4. Diffuse mycelium and degenerating trailing edge (arrowed) at the rear of the *C. nebularis* fairy ring (from Dowson *et al.*, 1989). Fig. 5. Mycelial mats of *Xylaria hypoxylon* (X) and mycelial tufts and rhizomorphs (R) of *Armillaria bulbosa* (A) produced from the surface of a slice cut from a beech log and incubated in a polythene bag (from Coates and Rayner, 1985b). Figs. 6,7. Melanized pseudosclerotial pads (arrowed) binding two hazel (*Corylus avellana*) branches (Fig. 6) and a hazel branch to a *Clematis* vine (Fig. 7) (from Ainsworth and Rayner, 1990) Figs. 8-10. Stages in the development of a foraging pattern produced by *Steccherinum fimbriatum* between an inoculum beechwood block and an uncolonized beechwood block bait respectively placed in the centre and to one side of a tray of unsterile soil (from Dowson *et al.*, 1988).

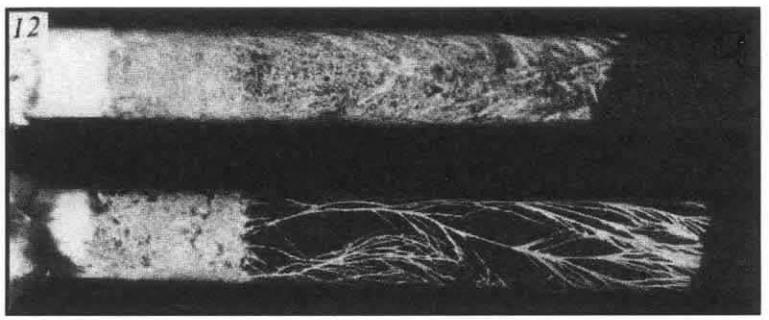
blocks colonized by cord-formers (e.g., Dowson *et al.*, 1986, 1988; Figs. 6-8) or mycorrhizal seedlings (e.g., Reed, 1984) and the mycelia will form foraging parties raiding out into (to them) unknown and unpredictable territory. Some mycelia don't even need to be uncovered. *Hymenochaete corrugata,* amongst others, traverses the canopy by forming mycelial bridges that bind together branches that have grown into contact (e.g., Ainsworth and Rayner, 1990; Figs. 9,10). A great many mycelia, inside and

outside the forest, have made a sandwich of photosynthetic cells, enabling them to grow, as lichens, on exposed surfaces.

When mycelial patterns are observed in these ways, it becomes apparent that much versatility springs from the ability of both the hyphal troops and the mycelial army — as a whole or in sectors— to switch their developmental mode to suit alternative states of functioning (Gregory, 1984; Rayner and Coates, 1987; Rayner and Franks, 1987; Rayner, 1991). At the level of individual hyphae, a well-known switch, evident in the phenomenon of yeast-mycelial dimorphism, determines whether development is determinate (cellular) or indeterminate and polarized (hyphal). Once hyphal tubes have been initiated, another switch, illustrated by some species of *Phlebia and Phanerochaete* (e.g., Rayner, 1991) determines whether hyphae are uncompartmented (coenocytic) or compartmented by septal partitions. Formation of septa is often correlated with formation of lateral branches, some of which may fuse (anastomose) when they collide, (time lapse photography by my colleague, Martyn Ainsworth has shown these collisions to be surprisingly forceful) and so convert the initially radiating developmental pattern into a network.

At the mycelial level, changes in branching pattern from frequent and at wide angles to infrequent and at narrow angles convert slowly-extending, dense colonies into rapidly extending, effuse ones, in a manner analogous to the gear shifts of a forward-driven motor vehicle (Fig. 11). Moreover, the hyphae may remain diffuse and separated from one another, or they may aggregate into compact structures, such as mycelial cords (Fig. 12), rhizomorphs, sclerotia, pseudosclerotia, stromata and fruit bodies. The formation of these aggregates is commonly correlated with another switch, from assimilative hyphae that actively take up organic nutrients to non-assimilative hyphae capable of developing outside an immediate food source. Finally, all or parts of the mycelium may become "senescent" or degenerative, leading to temporary or permanent cessation of extension, and often associated with reallocation of resources to survival, reproductive or explorative structures.

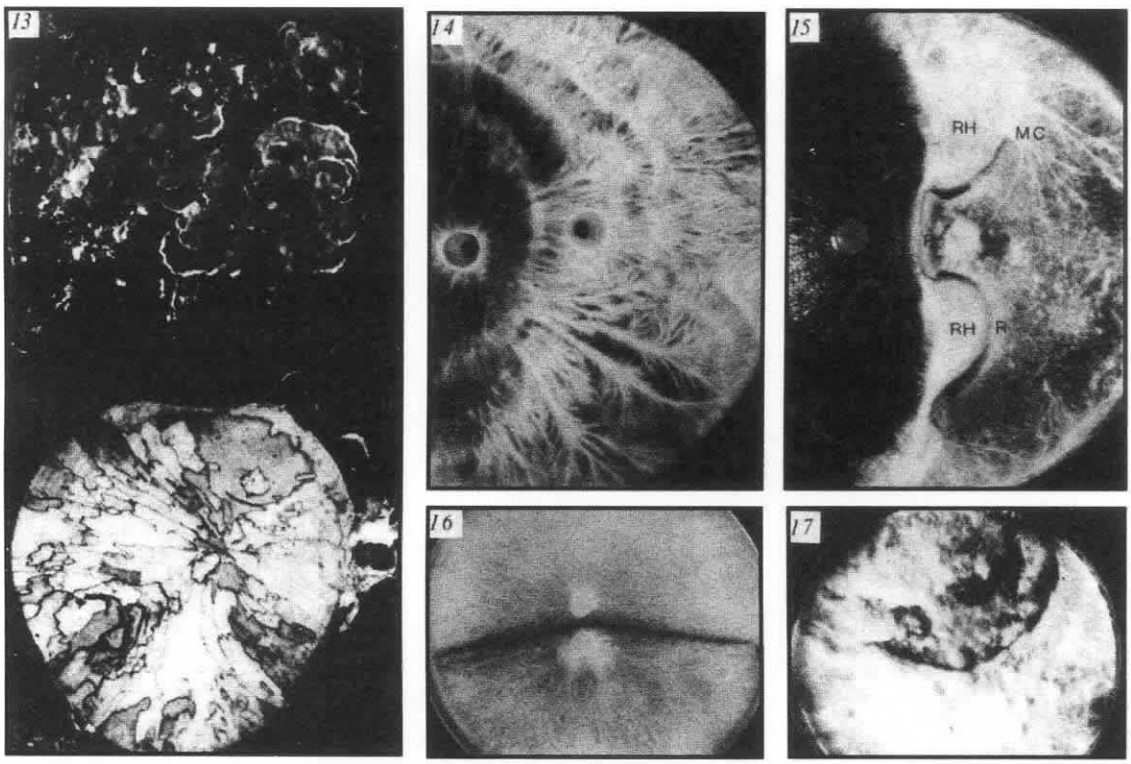




Figs. 11, 12. Alternative mycelial modes. Fig. 11. Slow-dense, fast-effuse and switching (sectoring) colonies of *Hypholoma fasciculare* on malt agar (from Rayner and Coates, 1987). Fig. 12. Diffuse (top tube) and aggregated mycelial systems of *Tricholomopsis platyphylla* growing respectively down tubes filled with sterile and non-sterile soil (from Thompson and Rayner, 1983).

By all these means, fungal mycelia generate a rich variety of developmental patterns. Another way in which they produce patterns, and one which also challenges their developmental versatility to the full, occurs when they encounter neighbouring mycelia. The outcomes of such encounters can often be seen directly in the field, in the mosaic structure of lichen, wood decay (Fig. 13), leaf-litter and other communities, and in clashes involving fairy ring- and mycelial cord-forming fungi. The encounters can also usefully be visualised in pure culture and in semi-natural systems, where they may provide valuable insights into mechanisms underlying mycelial versatility.

Encounters between the mycelia of different species of fungi can lead to interdigitation of hyphal systems, to long-range inhibition of one or both



Figs. 13-17. Mycelial interaction patterns. Fig. 13. Cut surface and underlying cross section of a decaying beech log showing demarcation of different individuals of *Coriolus versicolor* (forming fruit bodies on the cut surface) and other fungi into a mosaic of discrete decay regions (courtesy of Dr. D. Coates). Fig. 14 . Culture of *Hypholoma fasciculare* (inoculated left) invading *Phlebia rufa* by means of rhythmic mycelial mats and dendritic mycelial cords (courtesy of Dr. G.S. Griffith). Fig. 15. Interaction in culture between mycelia of *Phanerochaete velutina* (inoculated left) and Phlebia radiata. Rhythmic invasion fronts (RH) produced by *P. velutina* have been halted where *P. radiata* has produced ridges (R) of salmon-pink aerial mycelium, but these ridges have subsequently been penetrated by invasive mycelial cords (MC) (courtesy of Dr. G.S. Griffith). Fig. 16. Somatic rejection between single ascospore isolates from two different disease patches produced by *Rosellinia desmazieresii* (from Sharland *et al.*, 1988). Fig. 17. Complex outcome of nuclear exchange between homokaryons of *Stereum complicatum* from the USA (inoculated lowermost) and *Stereum hirsutum* from the USSR (courtesy of Dr. A. M. Ainsworth).

colonies due to production of diffusible and volatile antibiotics, and to "deadlock" reactions where, following contact, neither mycelium can invade the other's territory (e.g., Rayner and Webber, 1984). Especially interesting, from the point of view of pattern formation, are those wherevarious formations of presumably non-assimilative mycelium, supplied from behind, emerge at the interaction interface and either resist or effect invasion of the other colony. Some examples are shown in Figs. 14 and 15. Viewing the outcomes of these interactions, it is difficult to avoid thinking about their analogy to those following encounters between territorial armies on the one hand, and between immiscible fluids on the other.

When encounters occur between mycelia belonging to the same or closely related species, then, at least in ascomycetous and basidiomycetous fungi, attention turns to the events that follow hyphal anastomosis (hyphal fusion). Where anastomosis occurs between hyphae that are genetically identical, or, at least, not sufficiently genetically different to be recognized as "nonself", then, in the absence of self-inhibitory phenomena, the mycelia merge into a common network. What happens, though, when the mycelia are sufficiently different to be distinguishable as self and nonself? Anastomosis then provides a chance for the genes in one mycelium to gain "physiological access", that is, to draw and exploit resources from the other mycelium. It also provides an opportunity for "genetic access", that is for genes from one mycelium actually to invade the other's protoplasm. In terms of genetic survival and spread, nonself anastomoses, like attempted mergers between commercial corporations, represent a high-risk high-opportunity strategy. Potential benefits of increased territory and partnership are set against possible costs of disharmony, transfer of troublesome agents, loss of self-expression and loss of territory to an invader. Such prospects are of great evolutionary significance. To what extent, then, is the potential for physiological and genetic access, inherent in nonself anastomosis, actually realized in practice; and what are the consequences?

Sex and the Single Mycelium

Two extreme outcomes of nonself anastomosis are common. The first, nonself acceptance, provides the essential basis for sexual outcrossing in basidiomycetes (other than rusts, smuts and some jelly fungi). These organisms lack specialized sex organs and so are unable to keep their sexual and bodily (somatic) lives clearly separate. When individual basidiospores produced by sexually outcrossing populations of these fungi germinate, they produce primary mycelia, homokaryons, containing nuclei that are all derived (by mitotic division) from one original nucleus. When two such homokaryons meet and anastomose, then, providing that they contain complementary mating-type genes, the nuclei from one mycelium may be allowed to immigrate into the other and associate with resident nuclei. This process gives rise to a secondary mycelium which, in containing sets of nuclear genes (nuclear genomes) from two different genetic sources, is heterokaryotic (where the nuclear genomes remain

physically discrete, in separate nuclei) or, exceptionally, diploid — as in some species of *Armillaria*.

Important clues about the intracellular dynamics of basidiomycete mycelia can be obtained by observing the patterns of emergence of secondary mycelia from compatible matings between homokaryons. As applies to a road network emanating from a city centre, and as a direct consequence of the developmental history of the mycelium, two main access routes are available to immigrating nonself nuclei. Inward passage through the radial routes that are ultimately channeled through the colony centre itself requires erosion of septal partitions laid down prior to anastomosis. Lateral and outward passage may be effected through anastomoses and towards the apices of hyphae that may still be extending; in this case it may not be necessary to traverse septal partitions. The relative usage of these two main access routes determines the pattern of emergence of the secondary mycelium, which may either be localized to the interaction interface and the periphery of colonies, or it may be generalized through the entire body of one or both participating homokaryons. In the latter case, a physiologically integrated unit arises from the mating. Another important aspect of the pattern of emergence of secondary mycelium is that it commonly involves a change of mode, for example from slow-dense to fast-effuse development. Moreover, when emergence is localized, extension of the homokaryotic "parents" often ceases, suggesting that their offspring is somehow drawing on their resources (a familiar situation perhaps!).

In the many ascomycetes where sexual conjugation can be achieved in the secluded privacy of sex organs, outcrossing is not dependent on access of nonself nuclei through somatic anastomoses. Nonetheless, there is some evidence, for example, amongst the Xylariaceae, that somatic access may still be possible, and that it leads to emergence of heterokaryotic mycelia in patterns strongly reminiscent of those seen in basidiomycete matings (e.g., Sharland and Rayner, 1989). However, here the heterokaryons are generally unstable, often reverting to one or other of the homokaryotic types, which consequently gains territory from the other. Such behaviour casts an intriguing light on the possible evolutionary origins and significance of sexual conjugation as a takeover bid for genetic territory that ends in a mutualistic merger!

At the other extreme to nonself acceptance responses following hyphal anastomosis are the widespread nonself rejection or somatic incompatibility responses that resist genetic and/or physiological access. These responses prevent the formation of genetically and physiologically integrated "unit" mycelia of the kind and on the scale envisaged by, for example, Burnett (1976). They vary markedly in their expression, but often take the form, both in nature (e.g., Fig. 13) and in culture (Fig. 16), of very obvious demarcation zones, which commonly contain dark pigment and dead hyphae, between adjacent colonies. Quite commonly also, mycelium abutting or even within the demarcation zones changes mode, producing such structures as ridges of aerial mycelium, cord-like aggregates, pseudosclerotial plates, various types of sporophore and

sclerotia. The parallel between such effects and the degenerative mechanisms described earlier is therefore strong.

Somatic incompatibility helps in the detection of the boundaries between genetically distinct mycelial individuals or, to use a plant population biological term, individual "genets", and so enables the structural patterns of natural fungal populations to be mapped in space and time. These patterns directly reflect the dynamic processes involved during fungal colonization, and can be deeply informative about modes and mechanisms of arrival, establishment and spread of fungal genets and the way that natural selection affects them at different stages in their lives (e.g., see Cooke and Rayner, 1984; Rayner and Boddy, 1988).

Whether a rejection response or an acceptance response is expressed between two anastomosing mycelia depends partly on stage in the life cycle. In basidiomycetes, persistent rejection is typically expressed between heterokaryons and between homokaryons that for one reason or another are not competent to mate, whereas in ascomycetes it is expressed between homokaryons, whether or not they are competent to mate. Nonetheless, there may seem to be something of a paradox in that the same basic process, the recognition of nonself difference, has two opposite outcomes, rejection and acceptance. Moreover, it is common to observe both rejection and acceptance responses in one and the same interaction (e.g., see Rayner, 1991), with acceptance tending to be a feature of developmentally more "juvenile" hyphae and rejection a feature of developmentally more "advanced" hyphae.

The Road to Genomic Chaos?

Such situations suggest that the opposite trends for rejection and acceptance of nonself exist in a state of dynamic tension, such that small changes in circumstances may push the system over a threshold from one response to the other. The existence of such tension has deep evolutionary implications, not least impinging on our understanding of the origin of species. The general biological issue at stake concerns how it is that potentially conflicting genomes, brought together by mating or other means, can co-exist stably with one another—and if they cannot, what the mechanisms and consequences of the resulting instability are.

It is here that interactions between mycelia belonging to the same or closely related species of higher fungi provide a marvellous experimental test bed. Numerous anastomoses between continuous mycelial labyrinths result in the mixing of nuclei and mitochondria* from each participant. Whereas mitochondria seem to stay mostly within the vicinity of the interaction interface, nuclei migrate away from it, following the access routes described earlier. Consequently nuclei are mixed in variable cytoplasmic backgrounds. Since there are numerous anastomoses and numerous individual hyphae through which migration occurs, the associa-

*The organelles that are the major site of cellular metabolism and contain their own DNA, which is different from the DNA found in the nucleus of the same cell

tion of a particular combination of nuclear and mitochondrial genomes is not a once and for all experiment, as it is in the matings of most organisms, but one that is repeated many times. There is therefore a chance of finding out whether the repeated experiment has a variable or invariable outcome.

In some fully-compatible basidiomycete matings, such as those made between homokaryons from the same breeding population, the outcome does seem to be homogeneous, in that a stable, morphologically-uniform secondary mycelium emerges. However, particularly when crosses are made between homokaryons from geographically or ecologically isolated populations, the outcome can be very heterogeneous and unstable, and I am currently taking a considerable interest in these (e.g., see Rayner, 1991). One particular case involves an interaction between strains of *Stereum complicatum* from the USA and *Stereum hirsutum* from the USSR (Fig. 17). The Soviet strain, having made itself accessible to outside information (immigration of nonself nuclei), becomes unstable, splitting into innumerable domains from which some subcultures phenotypically resemble the Soviet progenitor and others resemble the American. My colleagues and I are getting evidence, using molecular biological methods of analysis, for both genetic mechanisms (change in DNA arrangement) and epigenetic mechanisms (variation in DNA expression — including the apparent suppression of entire genomes) underlying this chaos. However, we still need to do much more work before we can really be certain what is going on.

Conflicting Flows: Pressure, Insulation and Mitochondrial Executives

So what controls the diverse patterns that fungal mycelia exhibit in their versatile responses to their physical environment and neighbours? Are the underlying mechanisms as varied as their output, or is there a relatively simple logistic process that applies throughout, analogous to that operating in a computer which basically adds, subtracts, and compares two binary numbers but yet generates enormous diversity?

Currently, I sense that there is a common, simple theme running through all that I have described, based on the concept that fungal mycelia behave dynamically as flow systems. The idea I am working on is therefore that their heterogeneous, initially radiating and subsequently networked developmental patterns result from the way that mycelia develop and distribute hydraulic pressure through a deformable boundary, the hyphal envelope (wall plus plasma membrane). Development of pressure is ultimately due to active transport of solutes across the envelope, followed by uptake of water by osmosis. The interesting part is how this pressure is then channeled to yield varied developmental modes.

An irrigation engineer, plumber or electrician knows that the pattern of release of pressure to the environment, and hence the resulting pattern of flow exhibited by a system, depends partly on how great the pressure is,

and partly on how well insulated the system is. Insulation tends to ensure that the entities within the system remain associated with one another, whilst a lack of insulation allows them to dissociate. In order for flow to occur, the insulation has to be partial: a complete seal prevents the build-up and release of pressure; total absence of insulation allows instantaneous discharge. Therefore it is clear why, throughout biology, indeed throughout the universe, there is no such thing as absolute dissociation (individualism) or absolute association (collectivism), and that the patterns we see result from a dynamic interaction between these two opposite, but interdependent trends.

Fungal mycelia appear to make this point beautifully. When the pressure within the system is low, as in a spore beginning the process of germination, initial expansion is symmetrical, taking up the "slack." As soon as the pressure passes a critical threshold, asymmetries in the boundary become significant, causing expansion to become directional or polarized, as in the emergence of one or more germ tubes. Prevention of backflow, due to reversal of the pressure gradient following nutrient uptake, may then be achieved by formation of closable valves, in the form of septa. When the pressure inside the hyphal tubes exceeds that which, due to a relative lack of insulation, can be maintained without turbulence, they branch. Where branches converge, they may anastomose. Where parts of the system become more demanding, they draw resources from others. The pressure within the system maintains all its components, other than those which have become completely sealed off, in some degree of communication with one another.

It follows from the above scenario that the manner of insulation of hyphal systems dictates their developmental pattern. Here two properties of hyphal boundaries are important; their mechanical rigidity or deformability and their permeability. However, whereas much has been written about the former, particularly in relation to mechanisms of apical extension, the latter has received less attention.

When a hypha is actively taking up solutes from its environment, i.e., when it is actively assimilative, it follows that its insulation should be relatively weak, and therefore that it should be prone to branch. By contrast, if a hypha is located at a site free from assimilable nutrients (including where these have been used up), energy may be conserved by more effective insulation, which in its turn will improve the capacity of the hypha to act as a conduit and reduce its tendency to branch. Equally, if a hypha is located in a hostile environment, it would be useful if it could become non-assimilative, hence enabling it to bypass, tolerate and even break down (by extracellular enzymes) those physicochemical barriers which characterise the existence of most long-lived fungi. For example, the fungus could invade a living root in a non-assimilative mode prior to killing tissue and then switching over to an assimilative mode: exactly this pattern does seem to be shown by many fungi causing root disease.

Some procedural mechanism which enables mycelia to change their patterns of insulation in response to demand could therefore play a very major role in versatility. I suspect not only that such a mechanism exists,

but that its "controlling executive" is the mitochondrion (e.g., Rayner and Ross, 1991). The mitochondrion determines whether metabolic processes in the cell are channeled into production of chemical energy, in the form of adenosine triphosphate (ATP), the principal energy-storage compound of the cell, that can fuel the pumps allowing active uptake from the environment, or into the production of insulating materials that conserve energy*.

Many lines of evidence suggest this kind of argument may be on the right lines. Not least is the fact that mycelial interactions of the type I have described have been shown to be associated with increased phenoloxidase activity, and that metabolic uncouplers, such as dinitrophenol, can cause mycelia to respond in much the same way as they do to another mycelium (G.S. Griffith and A.D.M. Rayner, unpublished). Moreover, there is growing evidence that whereas the walls of hyphae growing away from their growth medium are coated with hydrophobic compounds, these compounds are either not produced by or are able to diffuse away from hyphae within the medium (J.G.H. Wessels, personal communication).

Epilogue

This story begins and ends with the need for observations. I started by describing *observations* of mycelial patterns, emphasizing the need to see these in their natural setting. I showed how these observations have led me to question how fungal mycelia organise themselves both in terms of their behaviour as whole systems, and in terms of the behaviour and interactions of their component organelles and molecules. I suggested ways in which fungi might control some aspects of their development which, to me, seem to accord with these observations. I now want to establish how well or how badly these suggestions explain patterns of mycelial behaviour in general, and for that more observations are necessary. Some of these may require techniques beyond the scope of the field mycologist. On the other hand, it is the field that is the ultimate testing ground both for fungi themselves, and for the ideas that we may have about how they work. Even in an age of advanced technology, the observations of the field mycologist therefore remain an essential component in advancing our understanding of mycelial patterns.

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* During this process, the pumps involved compete for ATP with the so-called second messenger systems that transduce environmental signals into a form which causes changes in cell behaviour. Moreover, if there is an increase in ADP (the less energy-rich precursor of ATP), then there is liable, by feedback, to be a compensatory increase in the glycolytic and pentose phosphate pathways leading into the Krebs cycle, and an increase in the rate of turnover of the Krebs cycle itself. Consequently the precursors for synthesis, via so-called secondary metabolic pathways, of a variety of compounds may build up. These compounds include many that are hydrophobic (water repellent) and hence liable to play a role in insulation. Some, including phenolics, may uncouple the mitochondrion's ability to use respiratory pathways to convert ADP into ATP, so enhancing their own production, and potentially leading to cell death. The phenolics themselves may be acted upon by phenoloxidase enzymes, capable of converting them, via highly reactive quinones and free radicals, into melanin, which is likely to be an important insulator in its own right.

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